

THE STRUCTURE OF ALLOTROPA

HERBERT F. COPELAND

The monotropoid genus *Allotropia*, with the single species *A. virgata* Torrey and Gray, was described by Gray (9) as "gathered on the Cascade Mountains of northern Oregon, by Dr. Pickering and Mr. Brackenridge, in the South-Sea Exploring Expedition under Commodore Wilkes." The "northern Oregon" of the time

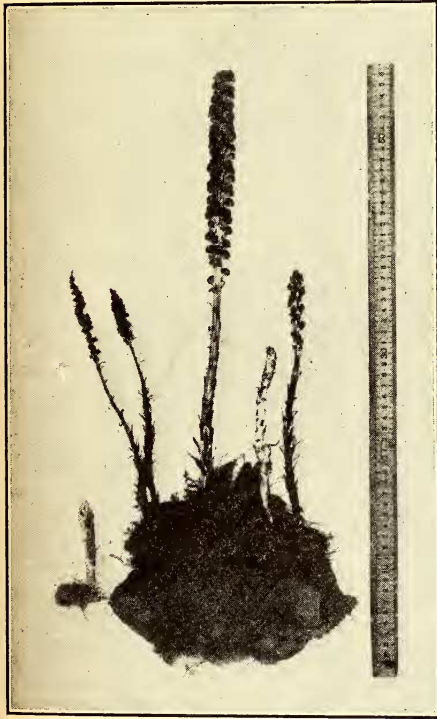


FIG. 1. *Allotropia virgata*. Plants collected on Mount Shasta, California, by William Bridge Cooke, September 8, 1936. Photograph by George C. Kimber.

of the Wilkes Expedition is of course the present State of Washington. The original publication just cited embraced all the essentials of taxonomic publication, the description of a genus, the name of a species, and the citation of a specimen; but it was brief and in a footnote; and a few years later Gray (10) presented a more extensive and formal account based largely on an adequate collection by Bolander, in the State Geological Survey, "in Mendocino County, between Little Bear Harbor and Noyo, 'generally near *Quercus densiflora*.'" The plant is now known to range from southern British Columbia through Washington and Oregon and south in California, in the Coast Range to Sonoma County and in the Sierra Nevada to Kings River. It occurs at altitudes from not far above sea level up to eight or nine thousand feet. The habitat of Bolander's collection caused Gray (11), and hence various European authors, to regard oak forests as the typical habitat of the plant. Actually, our tanbark oak is currently excluded from oaks proper, as *Lithocarpus densiflora*; and while *Allotropia* is often found as an associate of this plant, it is perhaps more often found in coniferous forests.

Allotropa invites superficial attention as being infrequent and at the same time conspicuous by its coloration in carmine and white. More fundamentally, it invites attention by certain peculiarities and uncertainties in its structure: authors have mentioned and again denied the presence of bractlets on the pedicel; there is a single whorl of perianth segments, interpreted sometimes as petals, sometimes as sepals (Gray adopted the former interpretation in his first mention of the plant, and the latter in his second); the anthers turn a half-somersault as the bud develops into the flower, agreeing in this feature with those of *Clethra* and *Pyrola* and differing from those of the other saprophytic Ericales; the flower has been described as lacking a disk. Interpretation of the characters affects, of course, opinion as to relationship. Gray associated the plant first with *Monotropa*, then with *Pyrola* and *Schweinitzia*, then with *Pterospora*. The more recent authorities, Drude (8), Andres (1), Domin (7), Small (14), and Jepson (13), have tended to separate it sharply from the other monotropoid plants, either implicitly by listing it first among the genera of the group, or explicitly by assigning it to a separate group of subtribal rank.

MATERIALS AND METHODS

The anatomical part of the present study is based upon two collections. Mr. Milo S. Baker of the Department of Botany, Santa Rosa Junior College, California, was so kind as to send a fresh specimen, collected about May 15, 1936, by Mr. McMillan of Annapolis, Sonoma County. It consisted of a single shoot without roots, in full anthesis. This collection is the basis of my understanding of the flower. Later in the same year, I had the good fortune to make the acquaintance of Mr. William Bridge Cooke, who was botanizing on Mount Shasta during the summer vacation. He kindly sent most abundant and excellent fresh material collected on September 8. It included abundant roots and nearly ripe fruits. My colleague, Mr. George C. Kimber, had the kindness to photograph this collection (text fig. 1).

After preliminary study, the material as received was fixed in Bouin's fluid. It was imbedded and sectioned in standard fashion. The staining combination generally used has been safranin and light green; this makes conspicuous the xylem and other tissue with lignified walls, and also cells containing stainable material which I take to be tannin. In studying ovules and seeds, in which lignified and tanniniferous cells are not of primary interest, a combination of acetocarmine and aniline blue was found useful. With the help and advice of Dr. A. S. Crafts and Dr. Katherine Esau, both of the College of Agriculture, University of California, Davis, a method of seeing the phloem clearly was worked out. The microtome sections are passed through xylol

and the alcohols down to water; exposed for some five minutes to 5 per cent H_2SO_4 ; flooded alternately with 0.1 per cent aniline blue and Crafts' (6) killing solution (KI, 0.75 g.; I, 0.5 g.; H_2O , 100 cc.), several changes of each, each for several minutes; and mounted and examined in Crafts' mounting solution (glycerine, 30 cc.; H_2O , 60 cc.; $ZnCl_2$, 2 g.; KI, trace; I, 0.2 g.). Such preparations are not permanent in the sense that they can be stored away and studied in subsequent years; but they will last for months, and even improve, at first, with age.

THE ROOT SYSTEM

As in other monotropoid plants, the root system is the permanent member of the plant, the shoots being temporary reproductive structures. The collection studied was from sandy soil and the roots were found fifteen to thirty centimeters below the surface. Roots are of all sizes from less than one millimeter to about four millimeters in diameter (pl. XXII, fig. 2). The smallest roots bear two rows of branches; the larger ones bear four rows. I have been unable to follow any of the larger roots to the tip; presumably they taper but little. In the microtome sections, only one tip of a small root was studied. A cap is present; as seen, it is minute, consisting of shrivelled cells whose remains are scattered along the sides of the root for a few millimeters back of the tip (pl. XXII, fig. 3). There is a definite dermatogen. There are no root hairs, and no mycorrhiza was detected. Spiral tracheids are formed to within a fraction of a millimeter of the tip; but the plerome cannot be said to reach to the dermatogen. The endodermis is not differentiated from the cortical parenchyma; accordingly, the boundary between the broad pericycle and the cortex cannot be recognized until considerable development has taken place. The oldest part of a root has a diarch primary xylem lying in a plane parallel to the axis of the parent root. Branch roots originate in the pericycle opposite the edges of the strand of xylem and grow out through the cortex; the boundary between stele and cortex is first evident by the level at which branch roots originate (pl. XXII, figs. 4, 5). The xylem of the branch root becomes connected to the primary xylem of the parent root. Apparently smaller roots remain diarch; larger ones, diarch at first, begin to develop a tetrarch xylem after forming their first branches, and subsequently form branches in four rows. A cambium forms secondary xylem, most abundantly in the angles between the four flanges of the primary xylem (pl. XXII, fig. 6). The primary xylem consists chiefly of scalariform elements opening into each other through scalariform or reticulate cross walls; with these are mixed many parenchymatous cells with non-lignified walls. The secondary xylem is of similar conducting elements and includes vascular rays in

some of which the cells are tanniferous. As the secondary wood appears, the line between stele and cortex becomes perceptible by an indefinable difference between the cells inside and outside a cylindrical boundary along which the walls of adjacent cells become more or less stainable with safranin. At this level, and in the planes where branch roots have already developed, adventitious buds appear.

I am not clear as to the timing of the development of which stages were seen. I suppose that growth in length and formation of branch roots takes place in early summer; that formation of secondary wood takes place next, and the development of buds in late summer; and that the shoots appear above ground, flower, and fruit, in the summer after their origin. Presumably each root bears only one crop of secondary roots, and only one crop of shoots, and then dies, leaving the space to the branch roots which it has produced.

These roots, in contrast to those of *Sarcodes* and *Pleuricospora* are perfectly normal; there is no question here of a procaulon. The absence of mycorrhiza may be associated with the sandy soil from which the material was collected (*cf.* Christoph (2)); and the presence of a root cap and the endogenous origin of the branches may in turn be associated with the absence of mycorrhiza.

GROSS STRUCTURE OF THE SHOOT

Each stem is unbranched and can be regarded as a peduncle together with the axis of a raceme. All of the foliar organs are essentially of the same nature, although the lower ones may be called leaves and the upper ones bracts in a raceme. When fresh and living they are white and fleshy, acute, usually entire below and more or less fimbriate above. They vary in size and shape in different zones of the shoot. They show small numbers of parallel veins evident as red streaks. They do not long remain fresh and white, but soon shrivel and turn brown or black.

The most conspicuous feature of the plant is the coloration of the stem. It is basically white but marked by a regular network of brilliant red bands (pl. XXIV, fig. 21). The junctions of this network lie at the insertions of the leaves; two lines converging from below join at each node, ascend the stem a short distance as a broad single line, and then diverge, running to the bases of the two leaves next above.

In most of the published accounts the shoots are described as rather short and divisible into a densely scaly lower part, a sparsely scaly middle part, and a bracted raceme. Some plants, however, are quite tall, and it is sometimes possible to distinguish other regions in addition to the ones just mentioned: if the roots are deeply seated, there may be a long slender stalk below the densely scaly portion; and the latter is sometimes divisible into

a lower region of short leaves and an upper region of longer ones. There is considerable variation in the relative sizes of these parts. The phyllotaxy is spiral, but it is commonly not an orthodox spiral: the numbers found by counting the files of scales on the same shoot, respectively to right and to left, are often not adjacent numbers of the 2, 3, 5, 8, etc., series; they are often not numbers of this series at all. Tables I and II present some frag-

TABLE I
Lengths in centimeters of various parts of shoots of *Allotropa*

Designation of shoot	Stalk below bulb	Region of compact scales		Peduncle	Inflorescence	Total
		Lower	Upper			
A	5	17	17	35
B	4	5	6	16	20	51
C	2.5	..	14	8.5	9	34
D	2	..	11	6	7	26
E	2.5	..	14	5	5	26.5
F	1.5	..	14	6	5	26.5
G	3	..	6	11	8	28
H	6	..	5	14	9	34
I	..	3	1.5	9.5	16	30
J	1.5	..	16	9	7	33.5
K	10	..	9.5	4.5	5	29

TABLE II
Numbers of parstichies to left (*l*) and right (*r*) in various parts of certain shoots of *Allotropa*

Designation of shoot	Region of compact scales		Peduncle	Inflorescence
	Lower	Upper		
A		15 <i>l</i>	5 <i>l</i>	6 <i>l</i>
			6 <i>r</i>	4 <i>r</i>
B	10 <i>l</i>	5 <i>l</i>	4 <i>l</i>	3 <i>l</i>
	7 <i>r</i>	7 <i>r</i>	3 <i>r</i>	4 <i>r</i>
Various other shoots of Cooke's collection		8 <i>l</i>		
		6 <i>r</i>		
		4 <i>l</i>		
		5 <i>r</i>		
			3 <i>l</i>	2 <i>l</i>
			5 <i>r</i>	5 <i>r</i>
			5 <i>l</i>	3 <i>l</i>
			5 <i>r</i>	5 <i>r</i>

mentary notes on these points. In these tables, shoot "A" is the one furnished by Mr. Baker; shoot "B" is the exceptionally tall one of Mr. Cooke's collection, shown in the middle of figure 1; the others are various other shoots of the latter collection.

ANATOMY OF THE SHOOT

By sectioning a fresh stem, one finds that the red pigment is confined to the epidermis (in the ovary and stigma it is found also in the next few layers of cells within). It is an indicator, turning blue in ammonia vapor and red again in hydrochloric acid vapor; evidently it is an anthocyanin. It disappears completely during fixation and imbedding.

In microtome sections the epidermis both of stems and of leaves is found to bear a thin cuticle with very fine lengthwise striations; to be without stomata; and to contain tannin in every cell.

The cortex and pith are of parenchyma with many scattered tanniferous cells.

The vascular cylinder is a typical siphonostele, such as we expect in woody plants rather than in herbs: it is broken by vascular rays (bands of parenchyma, frequently tanniferous) and by leaf gaps, but not by pith rays. At the very base of the shoot, the vascular cylinder is compressed parallel to the axis of the root which bears it, and is connected to the secondary wood of the root.

The xylem includes little clusters of spiral tracheids, more or less crushed as the stem matures, on the inner border; it consists chiefly of scalariform vessels with scalariform or reticulate cross walls. The phloem includes, beside much parenchyma, little patches of typical sieve tubes and companion cells; there is usually one such cluster between each two vascular rays. There are no more than traces of cambial activity (pl. XXIII, fig. 11).

In young shoots the pericycle outside the phloem is parenchymatous (pl. XXIII, fig. 8). Later, in shoots still underground but well developed and ready for flowering in the following season, one finds a heavy sheath of lignified fibers between the phloem and the cortex (pl. XXIII, fig. 9). In fruiting shoots, several layers of cells of the pith, not directly against the xylem but separated from it by a narrow band of parenchyma, are lignified, and form a sheath on the inner side of the vascular cylinder (pl. XXIII, fig. 10).

Each leaf trace consists of a single bundle leaving a gap in the vascular cylinder. Branch traces vary in character with height in the stem and stage of development; the variations parallel those of the fibrous tissue already mentioned. No branch traces are to be found in association with the lowest leaf traces of the shoot. In older material, from higher in the stem, branch traces exist as pairs of bundles running from the two sides of each leaf trace and ending under abortive axillary buds. A sheath, in the form of a trough-shaped band of fibers, lies against the outer side of the leaf trace, and an inconspicuous little strand of fibers accompanies each bundle of the branch trace (pl. XXIII,

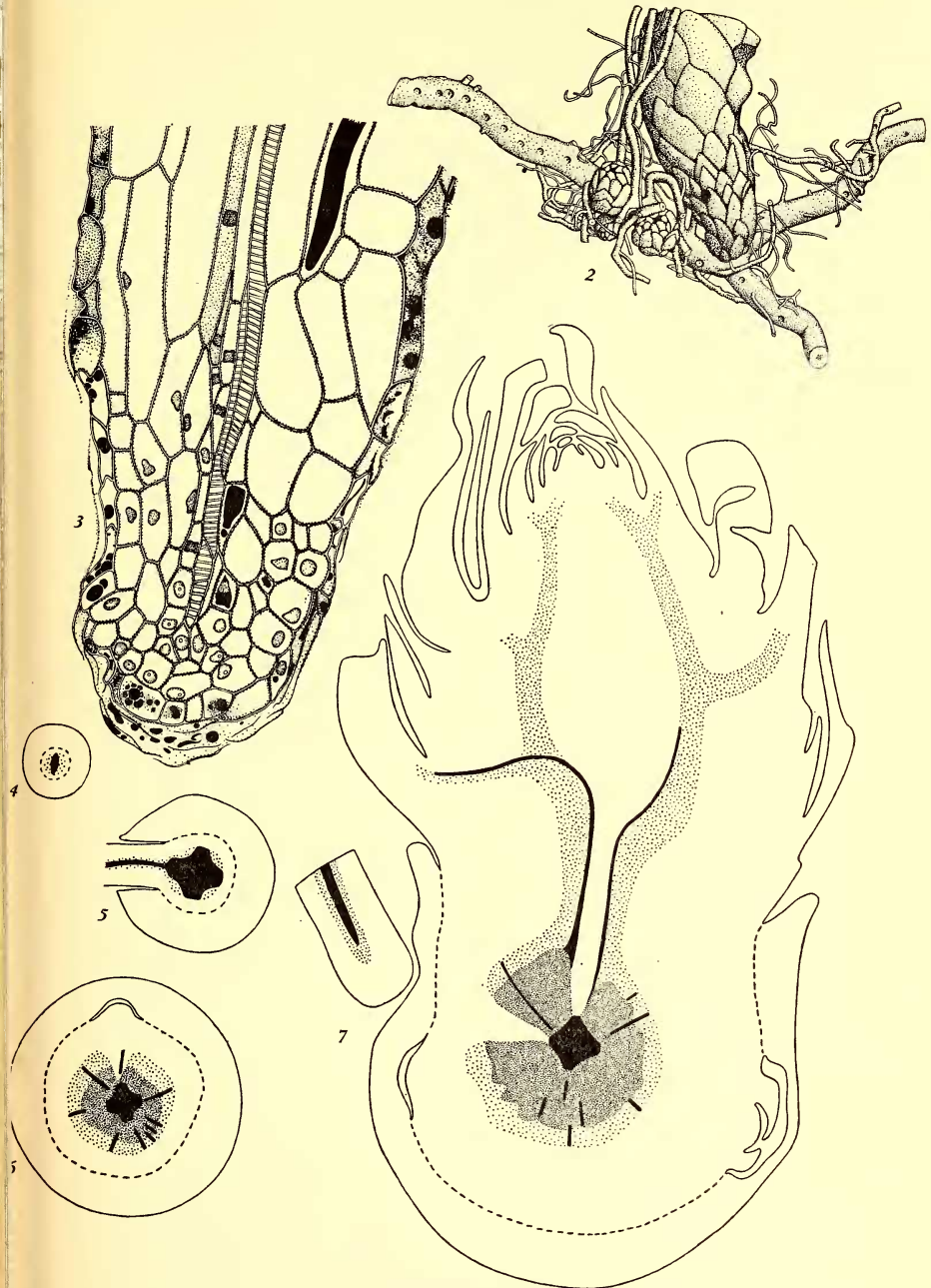


PLATE XXII. *ALLOTROPA VIRGATA*. Fig. 2. Roots and base of shoot $\times 1.6$. Fig. 3. Longitudinal section of root tip $\times 320$. Figs. 4, 5, 6, 7. Cross sections of roots $\times 16$; fig. 4, a small root with diarch primary xylem; fig. 5, a larger root showing tetrarch xylem and attachment of a branch; fig. 6, root showing secondary xylem and origin of a bud; fig. 7, root bearing a well developed bud. Primary xylem and tanniferous vascular rays black; secondary xylem heavily stippled; phloem and precambial tissue lightly stippled.

fig. 9). In the fruit-bearing rachis, leaf-trace and branch-trace (that is, flower trace) are united into a cylinder of tissue completely enclosed by a sheath of fibers (pl. XXIII, fig. 10). This body extends upward in the cortex through a distance of several centimeters before reaching the level of the bract and flower which it supplies (pl. XXIV, figs. 13-20. Note that in the models the vertical scale is only a quarter of the horizontal scale; these traces are exceedingly long and slender). At the level of the bract, the leaf trace escapes as several small bundles; here, in the inflorescence, the leaf trace appears as a minor appendage of the branch trace. The sheath may fade out at this level, or may continue into the pedicel; it fades out below the receptacle.

THE FLOWER

The pedicel in flower is white, approximately 1 millimeter thick and long. Referring to Bolander's collection, Gray remarked that "two subulate bractlets which were thought to have been detected upon the original specimen of *Allotropa* are not seen in the good specimens now in hand." Drude (8) and Domin (7) both write of these bractlets as definitely present. The fact is that they are present on some specimens, but absent from the majority, at least of specimens collected in California.

The five perianth segments (less commonly four or six) are white, more or less rhombic in outline, fimbriate, commonly a shade under 5 millimeters long and slightly wider.

There are twice as many stamens (pl. XXV, figs. 25-30) as perianth segments. The filaments are glabrous, dark, about as long as the perianth segments. The summit of the young filament is bent outward at a right angle and attached to the base of a dark anther about 2 millimeters long. This juvenile position is approximately the morphologically normal position of the anther; the outer side is the dorsal side. Even in the youngest material available to me, the anthers are dehiscing; each one opens through two lengthwise slits from the lower end half-way up the dorsal side. The slit in each lobe crosses the ends of both microsporangia of the lobe; the wall between them has already broken down in the youngest material I have seen. As the flower matures, the angle at the summit of the filament changes, the end swinging inward through ninety degrees, so that the anther hangs downward with the dorsal side inward and the slits at the top. If the anther is allowed to dry, the slits gape widely and appear as pores. A vascular bundle passes up within the filament, bending as the filament does; makes an additional right angle as it enters the anther; and traverses the middle of it, in the septum between the two lobes and in the plane of the septa between the two microsporangia of each lobe.

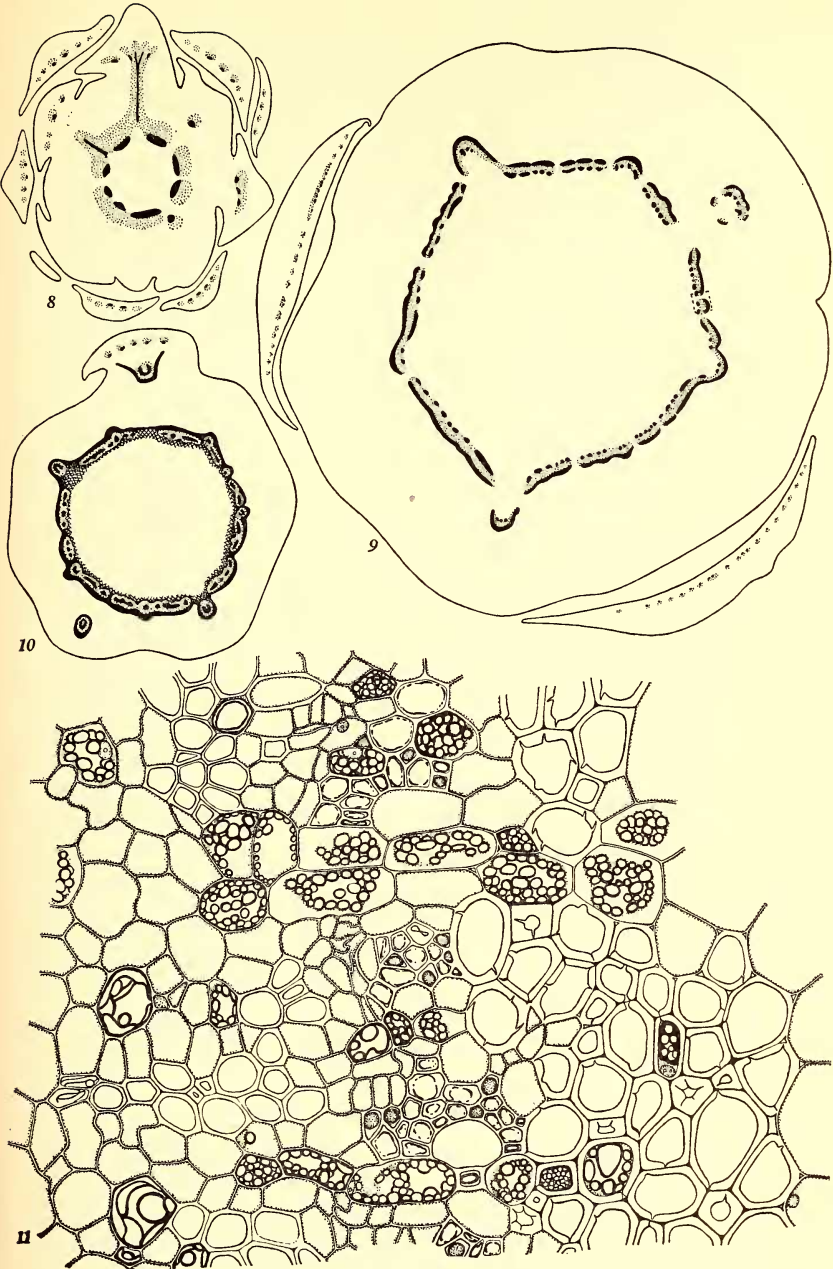


PLATE XXIII. *ALLOTROPA VIRGATA*. Fig. 8. Cross section of the base of a young shoot $\times 8$. Fig. 9. Cross section of a more highly developed shoot $\times 8$. Fig. 10. Cross section of rachis $\times 8$. Xylem and external sheath black; phloem and small-celled parenchyma within the xylem stippled; internal sheath cross-hatched. Fig. 11. Details of the cross section of the vascular cylinder, from the point indicated by the dotted square in fig. 9, $\times 320$.

The pollen grains are solitary and binucleate, in these respects being typical of the monotropoid group. In the material studied, most of them were found to be 3-grooved (pl. XXV, fig. 35); thus differing from those of *Pterospora* and *Pleuricospora*, which are usually 4-grooved.

The ovary is bright red, subglobular, and usually about 5 millimeters in diameter. It bears at the base a whorl of inconspicuous nectaries projecting between the bases of the filaments. It is impressed at the top, so that there is a groove about the base of the style, which is white, usually about 1 millimeter long and thick. The stigma is red, ordinarily about 1 millimeter high and 3 millimeters in diameter, obscurely 5-lobed (varying to 4- or 6-lobed); grooves, one on top of each lobe, converge at the center of the stigma on the opening leading to the interior of the ovary. In fresh material, the stigmatic surface is covered with a sticky fluid; microtome sections have shown germinating pollen grains imbedded in this.

In internal structure the ovary (pl. XXV, fig. 24) agrees with the other pyroloid and monotropoid plants which are said to show axile placentation: a cross section near the base shows five distinct locules, opposite the perianth segments, with a massive placenta projecting from a central column into each. Higher up, each placenta is split radially into two parts; the clefts between them radiate from a vertical channel continuous with the style channel. In this upper part, then, the placentation is really parietal, with the placentae thrust deeply into a single cavity. (What one calls a placenta in the lower part of the ovary is, as is usual in examples of axile placentation, the two edges of a single carpel; in the upper part, as is usual in examples of parietal placentation, it is the united edges of two adjacent carpels.) These placentae of the upper part, continuations of the septa between the cavities below, continue into the style as ridges projecting into the style channel. The lobes of the stigma stand above the grooves between them; each lobe is the end of one carpel.

The inner surface of the ovary wall is armored with a layer of sclerenchymatous fibers as in *Pterospora*, *Pyrola*, and *Chimaphila*, but not *Newberrya*, *Pityopus*, and *Pleuricospora*. The presence of this layer is associated with the dehiscence of a capsule, its absence with the production of a berry.

The stigmatic surface is covered with an epidermis of columnar cells, laterally in contact with one another, with the free ends domed outward. This is apparently a less specialized surface than those of *Sarcodes*, *Pterospora*, *Pityopus*, and *Pleuricospora*, in which these cells become spindly needles not in lateral contact with each other. These cells, and also several inner layers, but not the cells farthest from the surface, are tanniniferous.

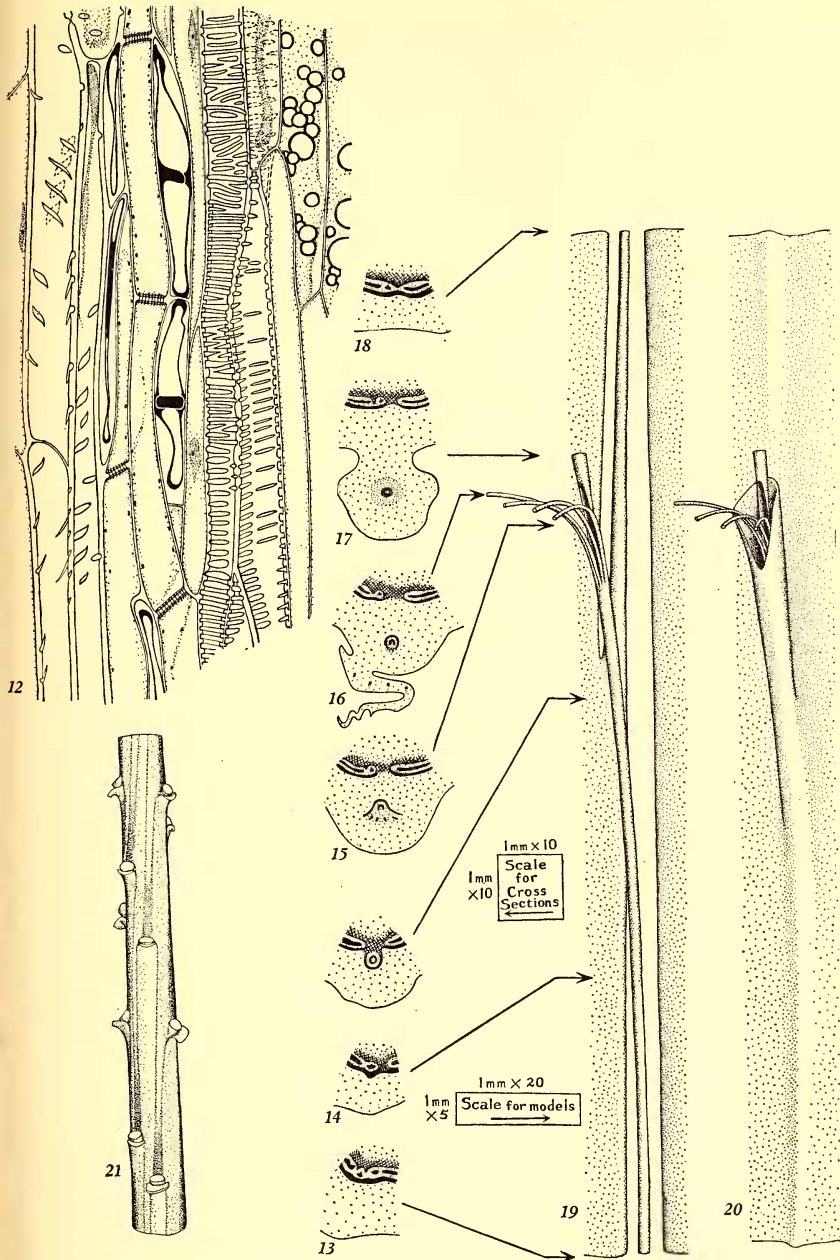


PLATE XXIV. *ALLOTROPA VIRGATA*. Fig. 12. Longitudinal section of vascular cylinder, from a stem comparable with those represented in figs. 9 and 11, $\times 320$. Figs. 13-18. Portions of cross sections of rachis in succession upward $\times 8$. Fig. 19. Model of a portion of the vascular cylinder of the rachis, based on figs. 13-18, not showing the sheath. Vertical scale $\times 4$; horizontal scale $\times 16$. Fig. 20. Similar model showing the sheath. Fig. 21. External view of the rachis $\times 1.6$.

The vascular cylinder in the pedicel in my material, which is without bractlets, shows no trace of bundles supplying them. The first whorl of five bundles in the receptacle forks periclinally, the lower branch running to a perianth segment, the upper to a stamen. The association of the perianth segment bundles with stamen bundles, and the location of the perianth segments opposite locules of the ovary, are features of petals as distinguished from sepals in the other monotropoid genera, and constitute proof that the perianth segments of *Allotropa* are petals. A second whorl of five bundles, alternating with the first, consists of stamen bundles. The remainder of the vascular supply of the flower breaks up, not without irregularity, into ten bundles. Five of these, lying in the planes of the petals, soon bend sharply outward and ascend the ovary wall; these are carpel dorsals. At the summit of the ovary, they bend down to the base of the style, then continue up the style in the thin places between the internal ridges; they end in the lobes of the stigma. The last whorl of five bundles, being in fact pairs of carpel ventrals, enters the central column of the ovary near the inner edges of the septa. They bend, branch, and break up in furnishing the vascular supply of the placentae. Branches of them may or may not run out through the septa to the ovary wall. In older flowers and in fruits, indefinite small numbers of bundles springing from the bases of the staminal bundles ascend the ovary wall for some distance between and parallel to the carpel dorsals. These correspond to the supernumerary bundles which puzzled me in *Pityopus*. They are evidently of no phylogenetic significance, but are developed in response to need, or by accident, in irregular positions (pl. XXV, fig. 36).

SEED AND FRUIT

Ovules ready for fertilization, and nearly ripe seeds, have been seen; the stages of development have not.

The ovules are typical of the monotropoid group. An ovule has an integument of two layers of cells; the nucellus is already

PLATE XXV. *ALLOTROPA VIRGATA* AND *PTEROSPORA*. Fig. 22. Bud from an underground shoot which would flower during the following summer $\times 40$. Fig. 23. Flower $\times 4$. Fig. 24. Dissection of a flower $\times 8$. Fig. 25. Two stamens from a bud $\times 8$. Fig. 26. Diagram of the anther of such a stamen to show the course of the bundle supplying it, the locus of the wall between microsporangia of the same anther lobe, and the plane of the section shown in fig. 34. Fig. 27. Similar diagram of a stamen in the mature position. Fig. 28. Mature stamen, lateral view $\times 8$. Fig. 29. Mature stamen, view from within the flower $\times 8$. Fig. 30. Mature stamen after dehiscence $\times 8$. Figs. 31, 32, 33, stamens of *Pterospora* $\times 8$, for comparison: fig. 31, ready for dehiscence; fig. 32, in process of dehiscence, lateral view; fig. 33, in process of dehiscence, view from outside the flower. Fig. 34. Cross section of anther at point of junction with filament $\times 40$. Fig. 35. Pollen grain $\times 800$. Fig. 36. Model of the vascular tissue in the receptacle approximately $\times 40$.

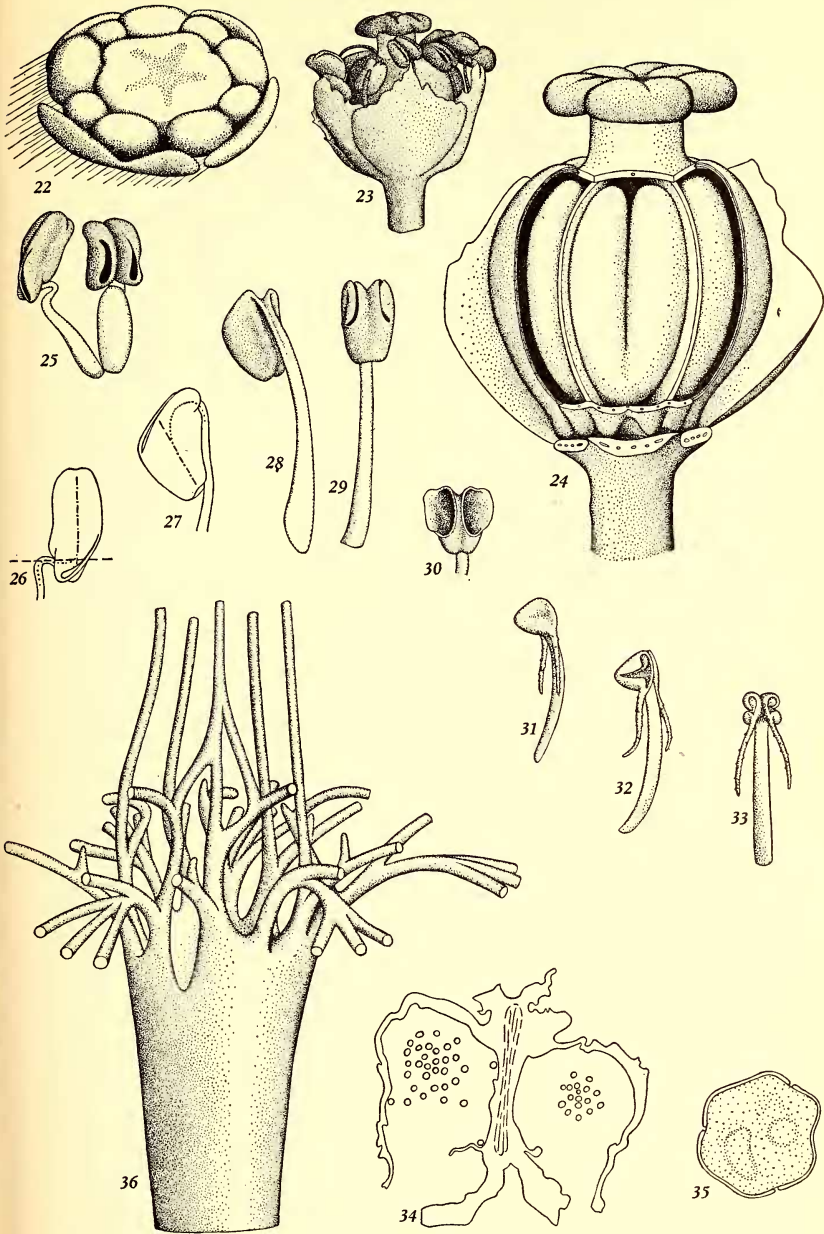


PLATE XXV. ALLOTROPA AND PTEROSPORA. (See explanation of figures on page 148.)

absorbed; the embryo sac consists of the usual egg, two synergids, endosperm mother cell, and three antipodal cells (pl. XXVI, fig. 40). The seed as a whole (pl. XXVI, fig. 42) is about 0.8 millimeter long; it shows a swollen middle part and a tail at each end; it is nearly white. Microtome sections (pl. XXVI, fig. 41) show that the integument, excepting the outmost layer of cells, tends to be absorbed or to collapse; that the endosperm has a haustorium at each end (the exact structure of the haustoria is not clear: they seem to consist of a few empty, very thick-walled cells); the endosperm proper few-celled, the cells well filled with granular material; the embryo, staining in the same fashion as the endosperm, 2- or 3-celled. There is probably a suspensor which is absorbed during development. The few cells of the embryo are separated by oblique walls, as if there were a terminal cell from which the others were successively cut off. I believe my understanding of the embryo of *Pleuricospora* as recently published (5) was incorrect. The embryo of *Pleuricospora* is of the same appearance as that of *Allotropa*, and presumably shows the same manner of growth.

The ovary seems to grow but slightly in developing into a fruit (pl. XXVI, figs. 37, 38). I have, indeed, some quite large fruits, about 1 centimeter in diameter; these are borne on an exceptionally large shoot, and are presumably developed from exceptionally large flowers. I have not observed dehiscence in nature. Fruits dried in the herbarium show two sets of lines of weakness, dehiscence taking place along both. Those of one set lie along the planes of the carpel dorsal bundles, and result in the ordinary dehiscence of a loculicidal capsule, as in *Pyrola*, *Chimaphila*, and *Pterospora*. The other set forms a circumferential line about the base of the style, as in *Sarcodes*.

DISCUSSION

The indefiniteness of various characters of *Allotropa*—in the relative development of the parts of the shoot; in the phyllotaxy; in the presence or absence of bractlets; and in the numbers of petals, stamens, and carpels—arouses speculation. One is tempted to interpret it in anthropomorphic terms as a resultant of a relaxation of discipline permitted by the dependent manner of nutrition. No scientific explanation of this indefiniteness is forthcoming: one is ignorant of the genetic and physiological mechanisms involved in such behavior, and of the manner of impact of natural selection such that these plants are free to vary much more widely than most.

This indefiniteness of character is itself a character of the whole monotropoid alliance. Variation in the nature of the calyx, discussed by Domin (7), is a phase of it. In perhaps a majority of the genera involved there is a perfectly definite calyx of four

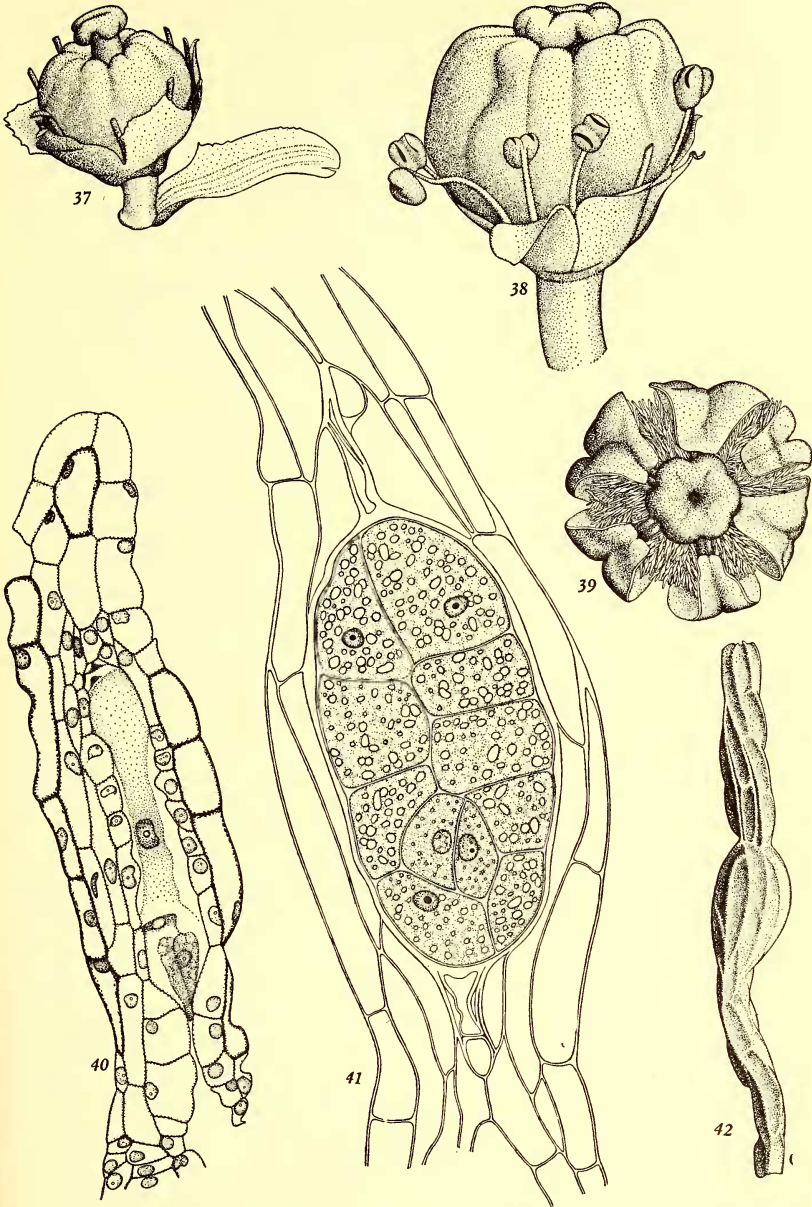


PLATE XXVI. *ALLOTROPA VIRGATA*. Figs. 37, 38. Fruits $\times 4$. Fig. 39. Summit view of a fruit in process of dehiscence (induced by drying and teasing with needles). Fig. 40. Ovule $\times 320$. Fig. 41. Longitudinal section of nearly mature seed $\times 320$. Fig. 42. Whole seed $\times 80$.

or five sepals alternating with the petals. In other genera, *Monotropa*, *Hypopitys*, *Newberrya*, and *Pityopus*, the number of sepals is variable, and the sepals tend to intergrade with leaves, bracts, or bractlets; buds and flowers may appear in the axils of the sepals of *Pityopus*, as of ordinary leaves. In *Allotropa* the calyx is completely suppressed, unless the bractlets, present on a minority of the specimens, are its representatives. As asepalous rather than apetalous, *Allotropa* is much less an anomaly than it has appeared to be. As I understand Domin's thesis, he suggests that the monotropid plants are primitively asepalous, and that a calyx (or pseudocalyx) has gradually been evolved from other foliar organs. I would be inclined to read the series in the reverse direction, and to understand first a loss in definiteness of numbers and sharp distinction of parts, and subsequently a loss of the sepals.

The stamens, and particularly the anthers, of *Allotropa* show resemblances in several directions; most obviously, with those of *Clethra*, *Pyrola*, and *Chimaphila*. In their mature position, they are the same as anthers of *Arbutus* and *Arctostaphylos*; but they lack the paired tails of the anthers of these genera. Finally, it is clear that anthers of *Pterospora* (pl. XXV, figs. 31-33) are essentially the same, although differing in being fixed in a horizontal position with the dorsal side upward. If *Allotropa* lacks the tails which anthers of *Arbutus* and *Arctostaphylos* possess, *Pterospora* has them. *Pterospora* shows another interesting feature: in addition to the slit along the proximal end of the anther, another is developed at right angles to this, along the plane separating the two microsporangia of each lobe. This gives a hint as to the evolution of the anthers of *Pleuricospora* and *Newberrya*, which open by lengthwise slits in this latter plane.

I have already pointed out resemblances in several directions as shown by the gynoecium. At this point one may offer some strictures on a recent paper by Hunt (12). This author assumes the evolution of carpels eventually from dichotomously branched thalli, and interprets them on this far-fetched basis. He recognizes two types, a more primitive 3-lobed type, exemplified by *Pyrola* (and other examples), and a more advanced 1-lobed type exemplified by *Clethra* (and again by other examples). The suggestion that the carpels of *Pyrola* and *Clethra* are of different types, and that the former is the more primitive is scarcely tenable. To me, it is clear from Hunt's figures that *Clethra* has a pistil comparable with those of other Ericales, but slightly more primitive; a less complete union of carpels is manifest in the fact that the single style passage usual in Ericales branches into three channels in the stigma of *Clethra*. The real difference is that in *Clethra* each lobe of the stigma stands at the end of a single carpel; in *Pyrola*, each lobe is compound, consisting of halves of the

ends of two adjacent carpels. This distinction is interesting: *Allotropa* and *Sarcodes* show the more primitive condition as does *Clethra*; the genera with fully parietal placentation, *Pleuricospora* and *Newberrya*, show as does *Pyrola* the derived condition.

The characters of *Allotropa*, as I have come to know them, seem to me to bind together to a surprising extent the genera of the Pyrolaceae of Engler and Prantl (the allies both of *Pyrola* and of *Monotropa*), a group so heterogeneous that their common origin has been questioned. As an asepalous plant, *Allotropa* cannot be recognized as the direct ancestor of the other Monotropoideae; but we can conceive it to be the living genus which has in most features diverged least from the extinct common ancestor of the group. The authors who have listed it first among the Monotropoideae seem fully justified.

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LITERATURE CITED

1. ANDRES, H. Piroleen-Studien. Verh. bot. Vereins Prov. Brandenburg 56: 1-76. 1914.
2. Christoph, H. Untersuchungen über die mykotrophen Verhältnisse der "Ericales" und die Keimung der Pyrolaceae. Bot. Centralbl. Beih. 38¹: 115-157, t. 8. 1921.
3. Copeland, H. F. The structure of the flower of *Newberrya*. Madroño 2: 137-142. 1934.
4. ————. On the genus *Pityopus*. Madroño 3: 154-168. 1935.
5. ————. The reproductive structures of *Pleuricospora*. Madroño 4: 1-16. 1937.
6. CRAFTS, A. S. A technique for demonstrating plasmodesma. Stain technology 6: 127-129. 1931.
7. DOMIN, K. Vergleichende Studien über den Fichtenspargel. . . . Sitzungsber. kgl. böhm. Gesellsch. d. Wiss., II Cl., I Stück: 1-111. 1915.
8. DRUDE, O. Pirolaceae. in A. Engler und K. Prantl. Die natürlichen Pflanzenfamilien 4¹: 3-11. 1889.
9. GRAY, A., JOHN TORREY, and J. S. NEWBERRY. Exogenous plants. Rep. Expl. Pac. R. R. 6³: 65-90. 1857.
10. GRAY, A. Characters of new plants from California and elsewhere. . . . Proc. Am. Acad. 7: 327-401. 1868.
11. ————. Synoptical Flora of North America, Vol. II, Part I. New York. 1878.
12. HUNT, K. W. A study of the style and stigma, with reference to the nature of the carpel. Amer. Journ. Bot. 24: 288-294. 1937.
13. JEPSON, W. L. Manual of the flowering plants of California. Berkeley. 1925.
14. SMALL, J. K. Monotropaceae. North American Flora 29: 11-18. 1914.